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LISIANTHIUS POLLEN FROM THE EOCENE OF PANAMA¹

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ABSTRACT

Fossil pollen similar to the extant genus *Lisianthus* (Gentianaceae) has been recovered from the middle(?) to late Eocene Gatuncillo formation, Panama. The genus presently extends from Mexico, through the Antilles and Central America, into northwest Colombia. The oldest fossil record for the family is from the Paleocene (pollen) and early Eocene (flowers) of the northern hemisphere. The distribution of modern Gentianaceae, and the meager fossil record, suggests the possibility of a northern origin for the family, migration of at least one member as far south as central Panama by the end of the Eocene, with subsequent introduction into northern South America. Since the Gentianaceae is relatively well represented in South America, it has been suggested the family is probably not a recent arrival. The occurrence of *Lisianthus* pollen in deposits as early as the Eocene in the region of present-day central Panama is consistent with this suggestion. The genus has not previously been reported in the fossil record.

During the Eocene the present region of Central America consisted of a series of volcanic islands trailing southward from the North American continent (Dengo, 1973). Extensive vulcanism is reflected in the Tertiary formations of Panama by the widespread occurrence of agglomerates (angular volcanic ejecta), tuffs (water-lain volcanic ash), and basalts (Stewart et al., 1980). Tectonic activity resulting from the interaction of the east Pacific (Cocos), North American, and developing Caribbean plates (Coney, 1982; Plafker, 1976) is equally evident throughout Cenozoic deposits in Central America. Along the Las Cascadas Reach of the Panama Canal, more than 113 faults have been observed in a distance of ca. 3 km (Stewart, pers. comm.). In the same region, left-handed fault motions total 4 km of displacement in a distance of 4 km. This tectonic activity resulted in the uplift of the isthmian region in latest Tertiary and Quaternary

times (Marshall et al., 1976, 1981, 1982; Webb, 1976). The biogeographic consequences of this event have been widely discussed (e.g., Gentry, 1982; Graham, 1973; Raven & Axelrod, 1974; Woodring, 1966).

Around the periphery of these islands mangrove swamps developed and their remains contributed to the formation of bands of lignite containing fossil pollen of *Rhizophora*, *Pelliceria*, and other genera. One such deposit is the Eocene Gatuncillo formation of Panama.

The Gatuncillo formation outcrops in south-central Panama east of the former Canal Zone. Near Alcalde Díaz, exposures consist of lignites interbedded between layers of claystone, siltstone, and fine-grained sandstone. Samples were collected from a 30-foot roadcut section and processed for plant microfossils. The lignites contained a diverse and well-preserved assemblage of fossil pollen and spores representing remnants

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of a vegetation that occupied the region ca. 40 million years ago.

The collecting locality is reached by a gravel road off the Boyd-Roosevelt Highway. The general area is shown on the Alcalde Díaz (Peñocito) quadrangle map (sheet 4243 11 NE) of the Army Map Service, and the specific collecting site at coordinates 100.8×660.8 on the recently compiled "Geologic Map of the Panama Canal and Vicinity" (Stewart et al., 1980).

The sediments near Alcalde Díaz represent a classic sequence of near-shore depositional environments. At other sites in the region the section is capped by a marine limestone, and marine limestones surround the locality. Thus the Gatuncillo lignites were deposited along an ancient shoreline that can be traced on the geologic map as the contact between the Gatuncillo formation and strata mapped as pre-Tertiary (Stewart et al., 1980).

The age of the Gatuncillo is late Eocene, although lower in the section some middle(?) Eocene sediments may locally be included. The age assignment is based on larger foraminifera reported by Cole (1952) and is accepted on the most recent version of the geologic map of Panama (Stewart et al., 1980). Almost all the species reported by Cole (1952) are upper Eocene foraminifera, but two (of 21) were known elsewhere only from the middle Eocene. These are *Yaberiella jamaicensis* Vaughan from the middle Eocene of Jamaica, and *Fabiania cubensis* Cushman & Bermúdez from Cuba and Florida. Consequently the age of the entire Gatuncillo sequence is regarded as middle(?) to late Eocene.

MATERIALS AND METHODS

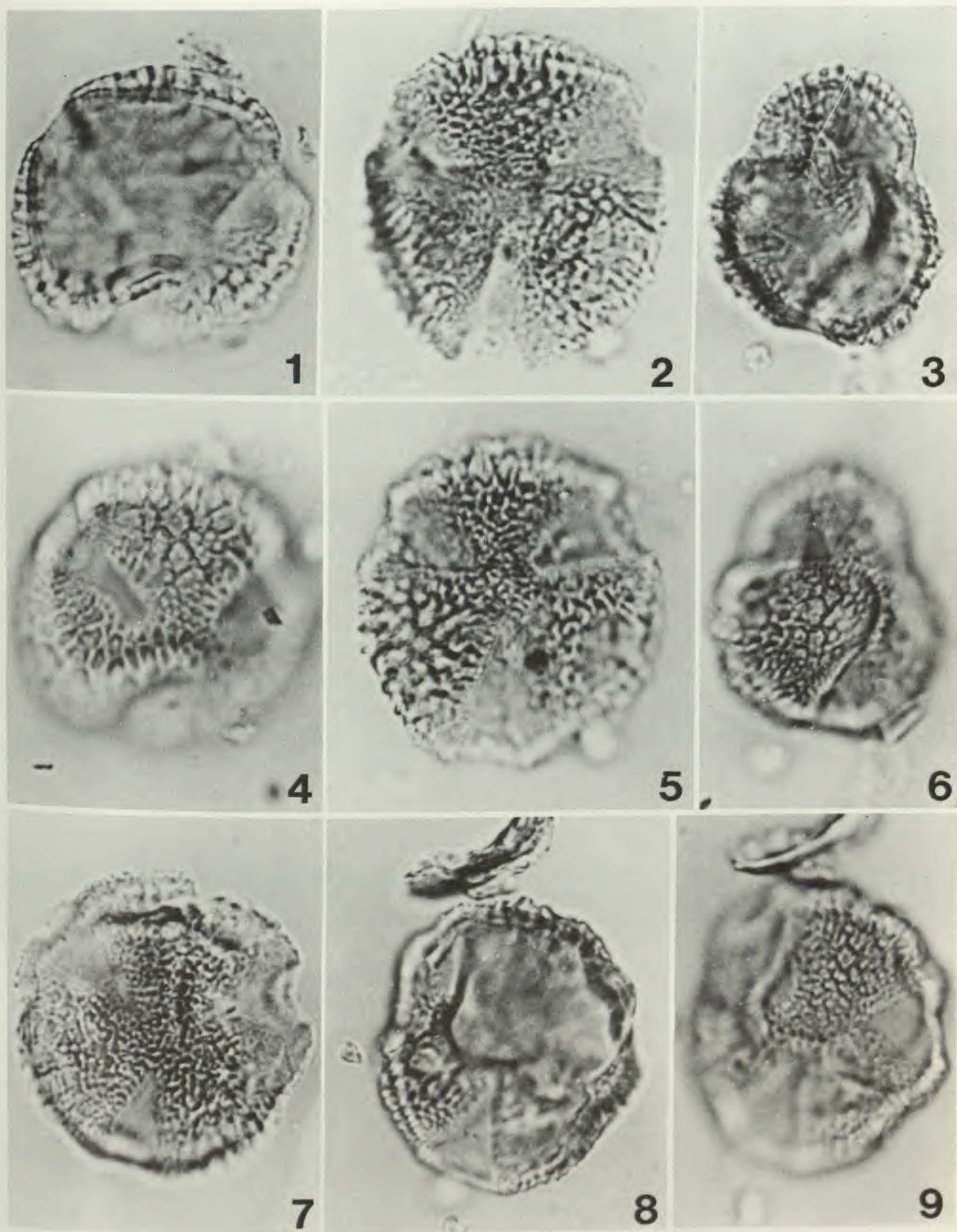
Lignite samples were macerated in a mortar and pestle then passed through HCl, HF, HNO₃, KOH, and acetolysis (one part concentrated H₂SO₄ to nine parts acetic anhydride). The palynomorphs were mounted unstained in glycerine jelly and sealed with CoverBond. Light photomicrographs were taken with a Wild microscope equipped with a Nikon 35 mm camera using Panatomic X film. SEM photomicrographs of extant pollen grains were prepared at the Smithsonian Institution. Acetolyzed samples were sputter-coated with gold-palladium and photographed with a Cambridge Stereoscan Mark IIA. The specimens are deposited in the palynology collections at Kent State University.

RESULTS

The fossil pollen and spores presently identified from the Eocene Gatuncillo formation of Panama include *Selaginella*, *Ceratopteris*, *Pteris*, Bromeliaceae, Palmae, cf. *Campnosperma*, *Ilex*, cf. *Arrabidaea*, cf. *Protium*, cf. *Tetragastris*, *Combretum/Terminalia*, *Casearia*, cf. *Tontalea*, *Alfaroa/Engelhardtia*, *Crudia*, Malpighiaceae, cf. *Ficus*, *Eugenia/Myrcia*, *Coccoloba*, *Rhizophora*, *Faramea*, *Cardiospermum*, *Serjania*, *Paullinia*, cf. *Chrysophyllum*, *Pelliceria*, and *Mortoniendron*. Also recovered were pollen grains described as follows (description of the microfossils is based on light microscopy at $400\times$ and $1,000\times$ oil immersion magnifications): Pollen oblate to oblate-spheroidal, amb circular; tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, tapering to acute apex, margin entire to slightly diffuse, faint margo formed by gradual diminution of reticulum near colpus margin, ca. $18\ \mu\text{m}$ long (equator to apex), extending within $6\text{--}7\ \mu\text{m}$ of pole (polar index 0.2), pore circular, situated at midpoint of colpus, margin diffuse, $4\text{--}5\ \mu\text{m}$ diam.; reticulate, reticulum somewhat irregular, diameter of lumen ca. $2\text{--}3\ \mu\text{m}$ in equatorial mesocolpal region, diminishing toward poles and margins of colpi, muri tall (ca. $2.5\ \mu\text{m}$) in equatorial mesocolpal area, giving somewhat deep, boxwork effect to reticulum, muri surface psilate, margins entire; exine tectate-perforate, height of columellae $2.5\ \mu\text{m}$ in equatorial mesocolpal region, diminishing toward poles and margins of colpi; size $35\text{--}45\ \mu\text{m}$.

A second microfossil similar to the one described above was recovered and differs only in having a slightly finer and more regular reticulum. The microfossils have a low but consistent frequency on the four slides counted, and constitute ca. 0.5% of the total assemblage. The description is based primarily on five well-preserved specimens from our Locality D (the Alcalde Díaz locality), sample 4 (near the base of the roadside section), slide 1 (slides labeled Pan D, 4-1), although other specimens were examined to establish size ranges in quantitative features. Specimens with the coarser reticulum were more common than those with the finer more regular reticulum (ca. 4:1).

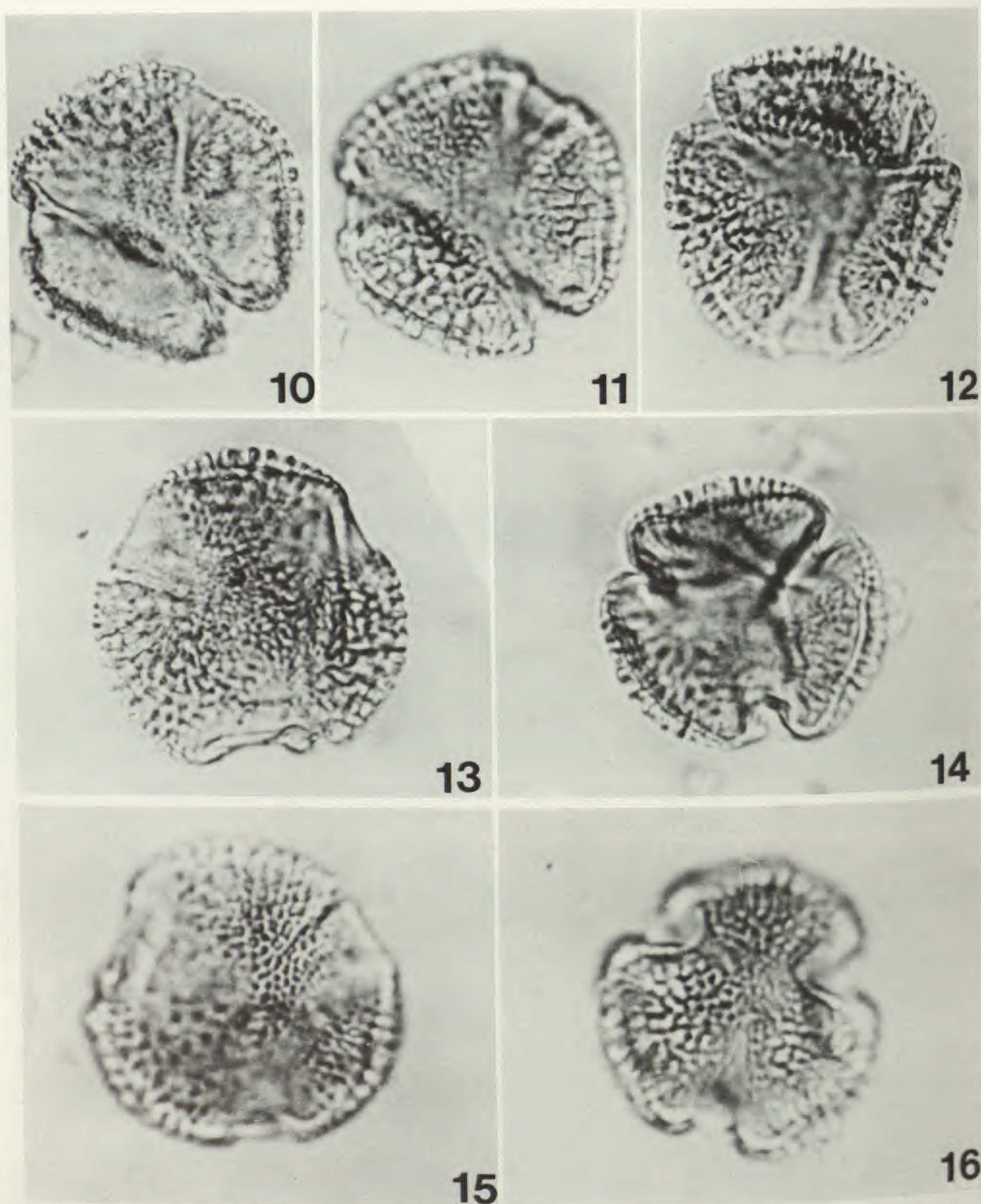
The modern genus in our pollen and spore reference collection most similar to the microfossils is *Lisianthus* P. Browne (sensu stricto). The collection includes all New World genera and most Old World genera of the Gentianaceae.



FIGURES 1-9. Fossil pollen of *Lisianthus* from the middle(?) to late Eocene Gatuncillo formation, Panama. — 1, 4. Pan D 4-1, England Slide Finder coordinates X-23, 36 μm . — 2, 5. Pan D 4-1, ESF V-34, 1, 45 μm . — 3, 6. Pan D 4-1, ESF Q-41, 3, 41 μm . — 7. Pan D 4-1, ESF Q-45, 45 μm . — 8, 9. Pan D 4-1, ESF O-39, 1-2, 38 μm .

and multiple collections for virtually all species of *Lisianthus*. The microfossils conform in all major morphological features to pollen of the modern genus, but differ slightly in shape. All the microfossils were encountered in polar or near-polar view, reflecting their oblate to oblate-

spheroidal shape. Most pollen grains of the modern species orient in equatorial view reflecting a prolate to slightly prolate-spheroidal shape. Also, the margo formed by diminution of the reticulum along the colpus margin is more pronounced in the modern pollen. These are minor, quanti-



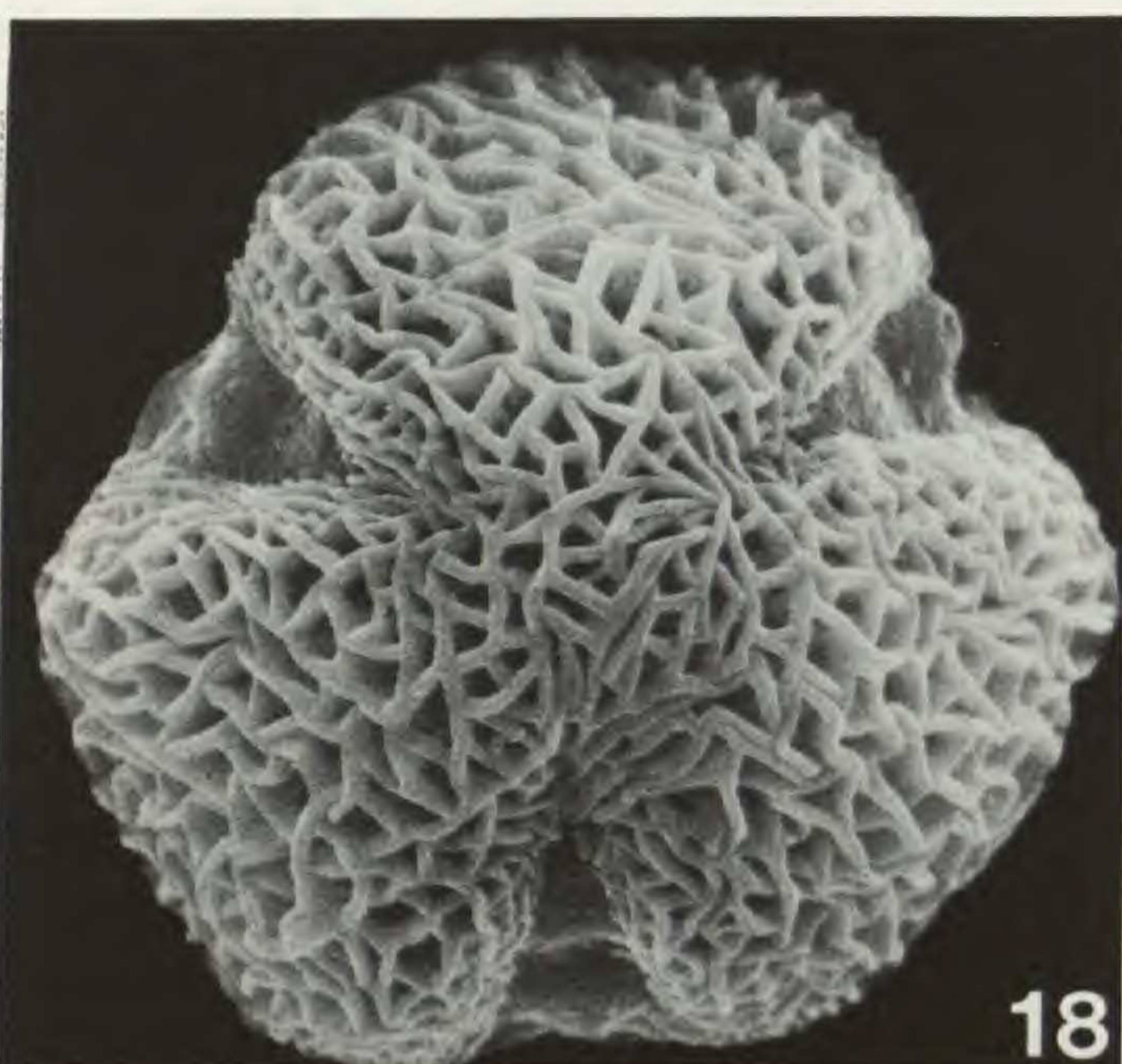
FIGURES 10–16. Light photomicrographs of modern *Lisianthus* pollen.—10–12. *L. glandulosus* A. Rich. (Ekman 1613, Cuba, K; Morton & Alain 9000, Cuba, K).—13–16. *L. nigrescens* Cham. & Schlect. (Breedlove 6477, Mexico, F; Ghiesbreght 702, Mexico, BM).

tative differences, however, and given both the overall close morphological similarity, and the age of the fossils (upper Eocene), the specimens are considered within the range of variation of extant *Lisianthus* pollen (cf. Figs. 1–9 and 10–16). SEM photomicrographs of extant pollen (Figs. 17–22) proved useful in confirming details of morphology and relating these to interpretation and identification of the microfossils.

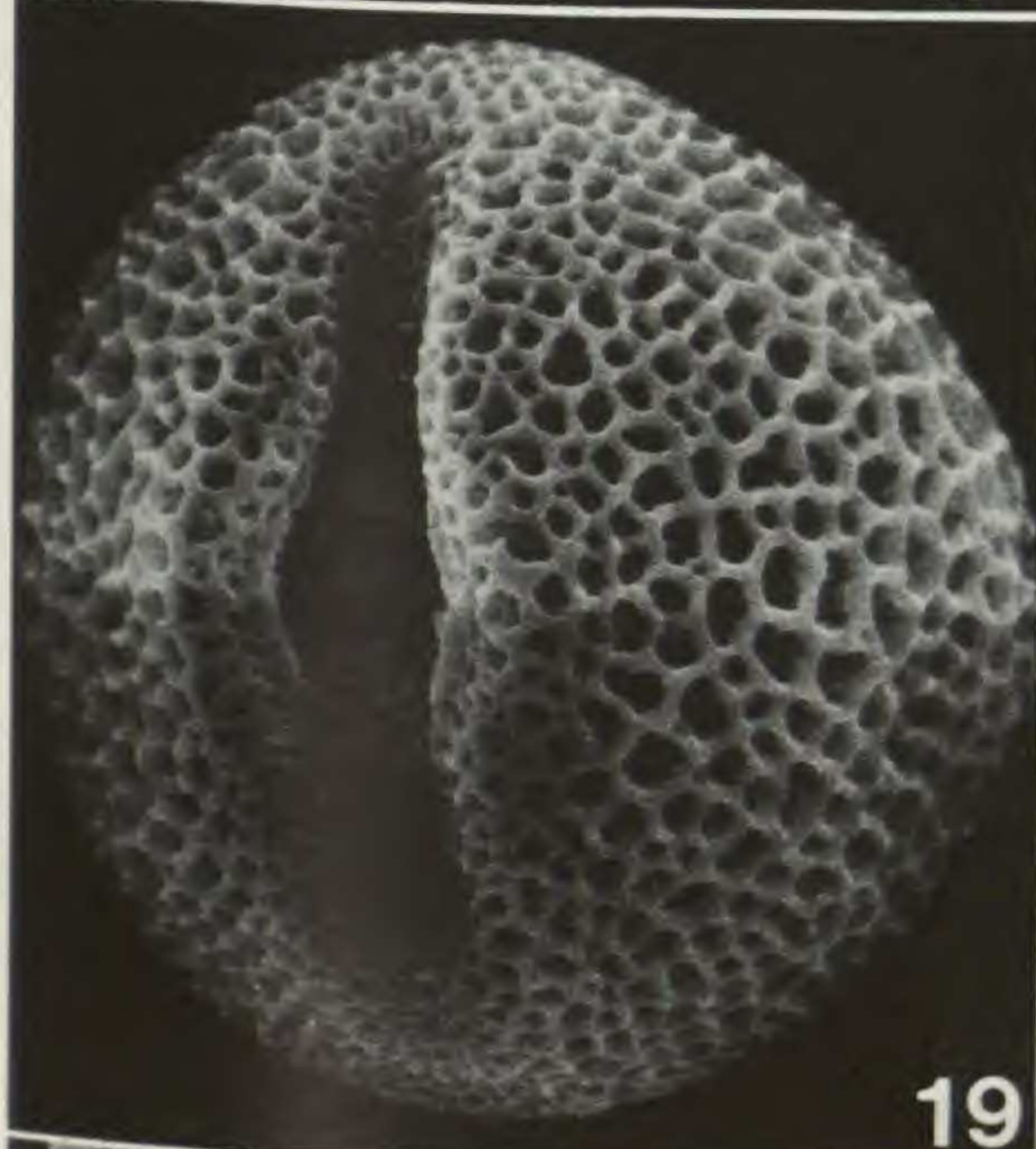
The modern pollen of *Lisianthus* (sensu lato) has been studied by Nilsson (1970a, 1970b; Nilsson in Elias & Robyns, 1975) and Weaver (1972). Among the species with pollen similar to the microfossils are *Lisianthus auratus* Standley, *L. capitatus* Urban, *L. dominensis* Urban, *L. glandulosus* A. Rich. (Figs. 10–12, 17, 19, 21), *L. nigrescens* Cham. & Schlect. (Figs. 13–16, 18, 20, 22), and *L. umbellatus* Sw. The variation in



17



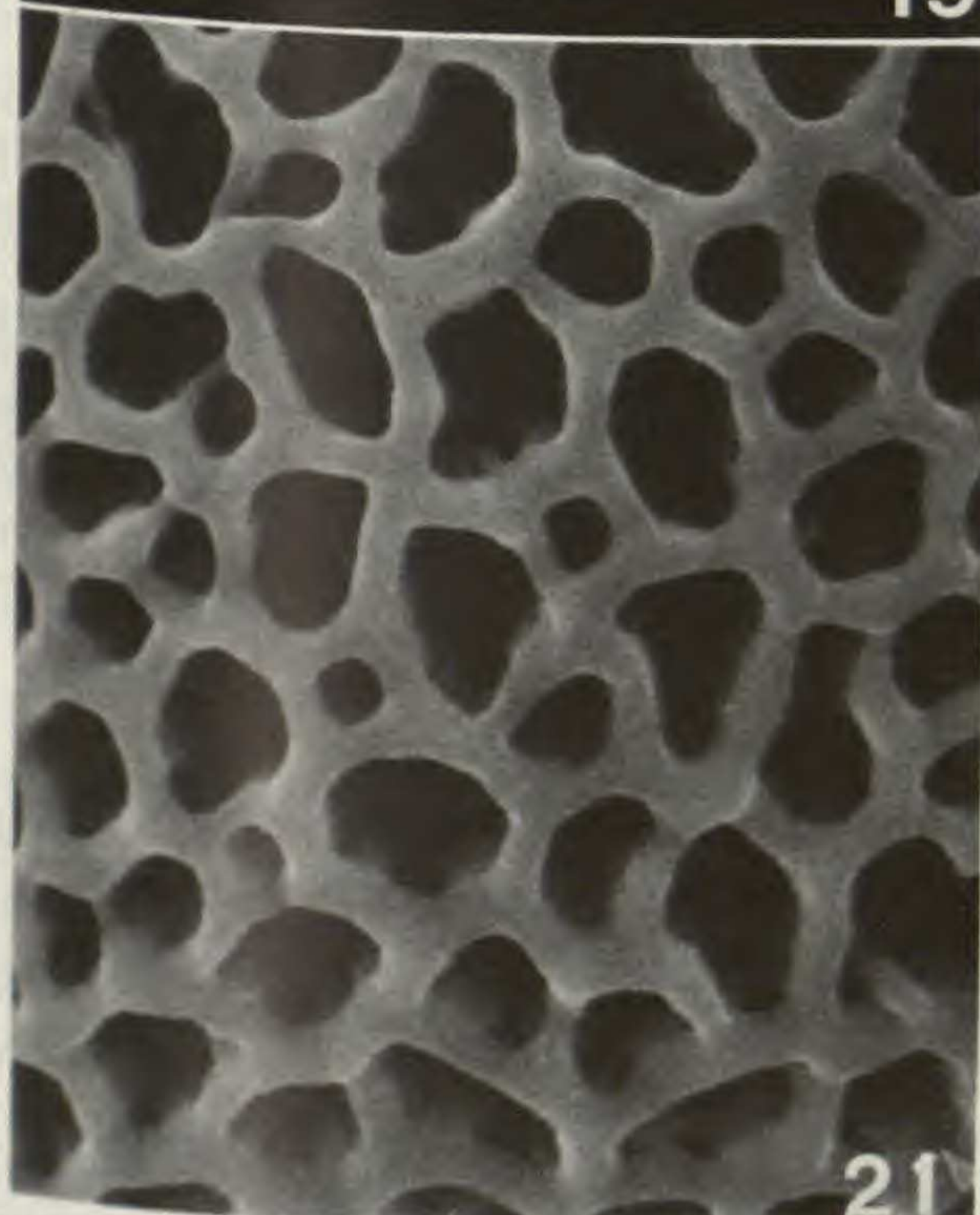
18



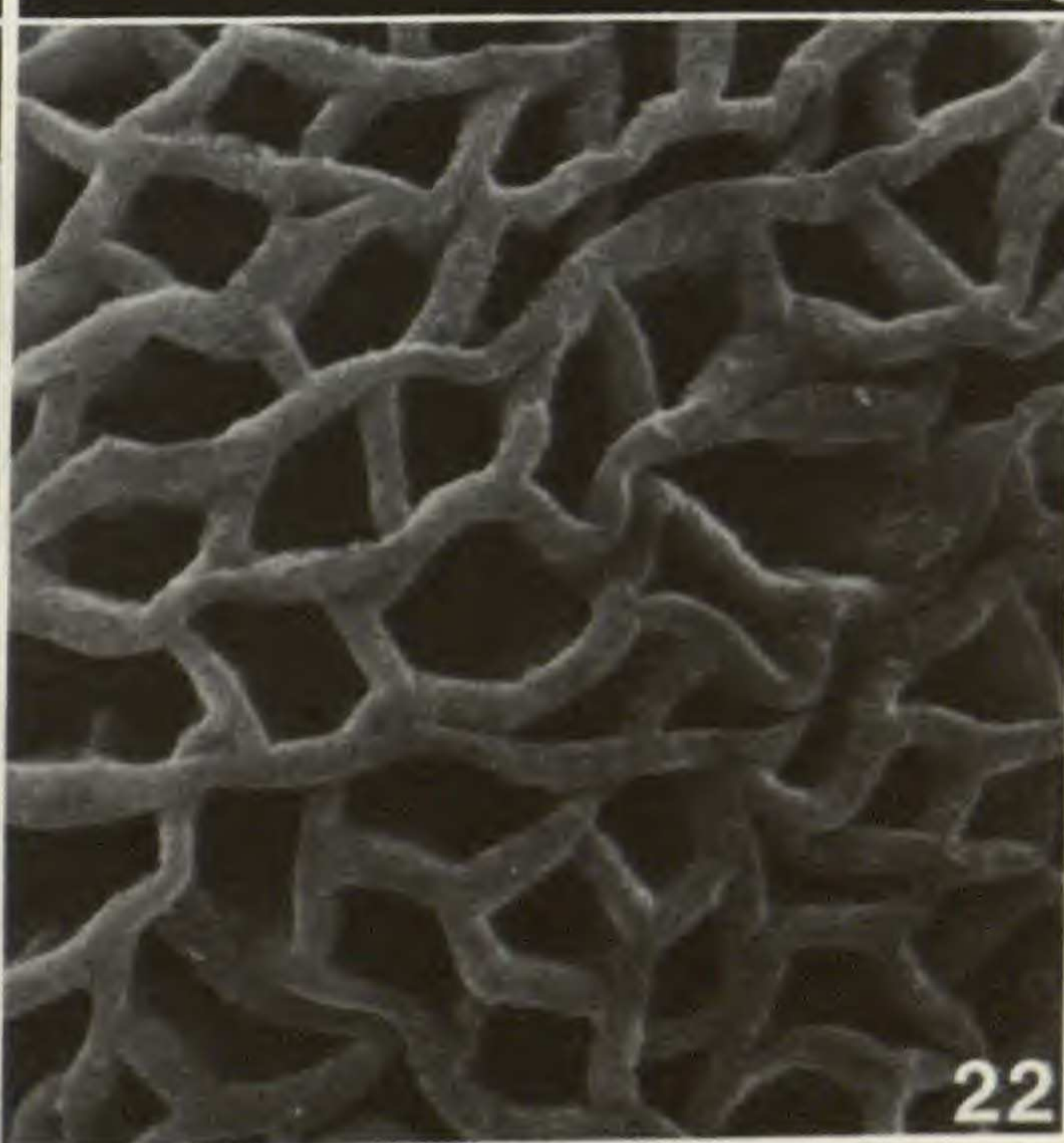
19



20



21



22

FIGURES 17–22. Scanning electron photomicrographs of modern *Lisianthus* pollen.—17, 19, 21. *L. glandulosus* A. Rich. (Morton & Alain 9000, Cuba, US).—18, 20, 22. *L. nigrescens* Cham. & Schlect. (Weaver 2183, Mexico, US).

fineness of the reticulum noted for the fossils is matched among the pollen of modern species of *Lisianthus*. Pollen of *L. nigrescens* is similar to the more coarsely reticulate microfossils, and *L. glandulosus* represents the more finely reticulate type.

Both Nilsson (1970a, 1970b; Nilsson in Elias & Robyns, 1975) and Weaver (1972) agreed that *Lisianthus* pollen can be distinguished from other genera of the Gentianaceae, and this finding is consistent with our survey of the family. For example, in the related segregate genus *Macrocarpaea* the grains are either in tetrads, or if in monads, they differ from *Lisianthus* by the presence of conspicuous gemmae, or by a more open reticulum (viz., greater diameter of the lumen) and/or slightly coarser columellae.

DISCUSSION

Lisianthus is a New World genus of 27 species and two varieties of perennial herbs, shrubs, and small trees distributed from south-central Mexico, through the Antilles and Central America, into northwest Colombia (Weaver, 1972). The genus has been monographed by Weaver (1972), and treated floristically by Elias and Robyns (1975) for the Flora of Panama. Recently Sytsma et al. (1983) have studied the phylogenetics of the *L. skinneri* complex by endonuclease DNA mapping, morphology, flavonoids, and allozymes. The plants are entomophilous, but small percentages of pollen are quite likely to enter depositional basins. The conspicuous flowers are borne in clusters of about 15 to 30, and there may be between six and ten clusters per plant. At maturity the anthers extend beyond the corolla. *Lisianthus seemannii* (Griseb.) Perkins is especially floriferous with 100 or more flowers per plant, and *L. skinneri* (Hemsl.) O. Kuntze, the most common Central American species, also flowers profusely. Furthermore, several species of *Lisianthus* form thickets that locally dominate the habitat. As noted by Germeraad et al. (1968), outwashing is an important means of pollen transport in tropical environments and accounts for the greater representation of pollen from entomophilous species in tropical sediments than in deposits from temperate regions.

Lisianthus occurs from near sea level to about 1,800 m and is found in a wide variety of habitats. For example, *L. saponarioides* Cham. & Schlect. grows from 600 to 1,200 m on rocky

limestone hillsides and in secondary scrub; *L. meianthus* Donn. Sm.—near sea level to 1,500 m in pine forests, limestone thickets, and roadsides; *L. oreopolus* Robins.—100 to 1,800 m in dry to moist pine or mixed forests; *L. peduncularis* L. O. Williams—dense moist forests at 1,000 m; *L. jefensis* Robyns & Elias—850 to 900 m in cloud forests; and *L. auratus* Standley—sea level to 1,800 m in pine forests or savannahs. Thus the floral features of *Lisianthus*, its occurrence in dense thickets, and its widespread distribution at moderately low elevations throughout Central America are consistent with the high-frequency, low-percentage recovery of microfossils from the Gatuncillo formation.

The presence of *Lisianthus* pollen in the late Eocene Gatuncillo formation, and earlier records of the Gentianaceae in the Paleocene and lower Eocene of the northern hemisphere (Crepet & Daghljan, 1981), is consistent with a northern origin for the family, one member of which had reached the area of present-day central Panama by late Eocene times. Its occurrence there at least raises the possibility of an early introduction from North America into South America prior to the more extensive exchange at the end of the Tertiary. This possibility parallels the similar impression of Raven and Axelrod (1974:629) based on the affinities and biogeography of modern taxa: "Judging from their affinities, the following taxa may also have gone from North America to South America. They are so well represented there it seems probable that they are not very recent arrivals: Boraginaceae, Clethraceae, Gentianaceae, Hydrophyllaceae, Loganiaceae—*Buddleia*, Onagraceae—*Fuchsia*, Plantaginaceae, Polemoniaceae, Scrophulariaceae, Theophrastaceae, Viscaceae."

Further consideration of the historical biogeography of *Lisianthus* and the Gentianaceae should await results of studies currently underway on other fossil microfloras from Central America. These include the lower Miocene Culebra, Cucaracha, and La Boca formations of Panama; the upper Miocene to Pliocene Gatun formation of Panama; and the Gatun formation in Costa Rica (Graham, unpubl. data). To date only the Culebra assemblage has been surveyed and *Lisianthus* pollen has not been recovered. Fossil representatives of other Gentianaceae have been discussed by Crepet and Daghljan (1981). This is the first report of *Lisianthus* in the fossil record.

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